POLAROTAXIS IN COPEPODS. I. AN ENDOGENOUS RHYTHM IN POLAROTAXIS IN CYCLOPS VERNALIS AND ITS RELATION TO VERTICAL MIGRATION

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In many terrestrial arthropods, the ability to detect polarized light is used to find geographical directions by means of sky polarization patterns which change with the sun's position in the sky (von Frisch, 1948; Pardi and Papi, 1953a, 1953b; Birukow, 1954; Vowles, 1955; Wellington, 1955; Papi, 1955). Such direction-finding is actually a special extension of the sun compass and requires that the organism possess a physiological clock to correct for the sun's movement through the sky and the concomitant changes in sky polarization.

The functional significance of polarized light sensitivity for planktonic animals has yet to be demonstrated. However, many such organisms can perceive polarized light (Baylor and Smith, 1953; Jander and Waterman, 1960) and polarization patterns are indeed present in the aquatic habitat (Waterman, 1954; Waterman and Westell, 1956; Ivanoff and Waterman, 1958; Ivanoff, Jerlov and Waterman, 1961). It is reasonable to speculate that these aquatic organisms use the polarization pattern of their environment for orientation just as do their terrestrial counterparts. This paper presents evidence that the natural pattern of polarization in the aquatic habitat is used as a frame of reference for swimming orientation in the copepod *Cyclops vernalis* and that the orientation of this animal to the plane of polarization changes rhythmically throughout the day in an ecologically meaningful way.

General Behavior

Material and Methods

As experimental animals, the fresh-water copepod *Cyclops vernalis* Fischer, collected in Clark's Pond near New Haven, Connecticut, was cultured at 20° C. in an aerated five-gallon aquarium in a darkroom having a 12-hour light, 12-hour dark cycle of illumination. Animals had lived in this culture for more than a month before experiments were begun.

To measure phototactic responses, 20 copepods were placed in a rectangular, clear Plexiglas vessel. One-half of this vessel was lined and covered with black Plexiglas to shield this half of the container from the overhead tungsten filament light source. An intensity of light set at 1100 lux was chosen to be the value incident at the water surface since this is a daylight intensity level commonly found in natural waters (Harris and Wolfe, 1955). The phototactic sign of the copepods was determined by measuring their preference for the light or dark half of the vessel at various times of day. The number of copepods in the light half of the vessel was recorded every 20 seconds over a period of 10 minutes, permitting an

average to be calculated. These observations were made at 2-hour intervals over the course of the 12-hour light period.

To ascertain geotactic responses, 20 copepods were placed in a 500-ml. graduated cylinder in complete darkness; there was no light-dark cycle. The copepods were observed with a red light at all times of the day to determine their distribution in the vessel. The number of copepods in the top third, middle third and bottom third of the vessel was recorded at 20-second intervals for 10 minutes. These observations were made at 2-hour intervals during the course of a 24-hour day.

Results

The copepods were photonegative at all times during the 12-hour light period, spending 90% of the time in the dark. When an occasional animal would venture into the lighted half of the vessel, it remained at the bottom and seldom swam upwards toward the light. There was no evidence for changes, rhythmic or otherwise, in phototactic sign.

The copepods were also geopositive at all times of day, spending 85% of the time on the bottom of the graduated cylinder. Again, there was no evidence for changes in geotactic sign at any time of the day.

It was also observed that when swimming horizontally in the water, *Cyclops vernalis* directed its ventral surface upward toward the overhead light. If light was shined from below, the ventral surface then faced downward, still toward the light. This behavior indicated that a ventral light reflex was present. When swimming vertically upward, the anterior end always led with the long axis of the body vertical. When the copepod moved downward, it either actively swam with its anterior end downward and long axis of the body vertical or it passively sank with its body axis horizontal.

Cyclops vernalis tended to cling to the sidewalls and bottom of any experimental vessel and often adhered to the water-air interface when one was present. It sporadically swam freely in the water. This behavior in the laboratory agrees with the field behavior as reported by Pennak (1966). Thus *Cyclops vernalis* is essentially restricted to vegetation in the littoral zone of lakes and ponds, being seldom found in the open water. It is a browsing species that often leaves the substrate to cruise about in spaces among the vegetation. This suggests that the copepods in the laboratory culture were in normal physiological condition.

POLAROTACTIC BEHAVIOR

Methods

The apparatus used to measure polarotaxis was similar to that employed by Bainbridge and Waterman (1957). A shallow cylindrical Plexiglas cell, 26 mm. deep and 108 mm. in diameter, containing 20 copepods, was illuminated from above by a vertical beam of linearly polarized light whose plane of polarization could be altered at will. The light originated from a tungsten filament lamp and passed successively through a focusing lens system, a heat filter, a depolarizer, a rotatable Polaroid linear polarizer, the experimental cell and finally through two lenses which produced an image of the copepods on a sheet of paper on the bench beneath.

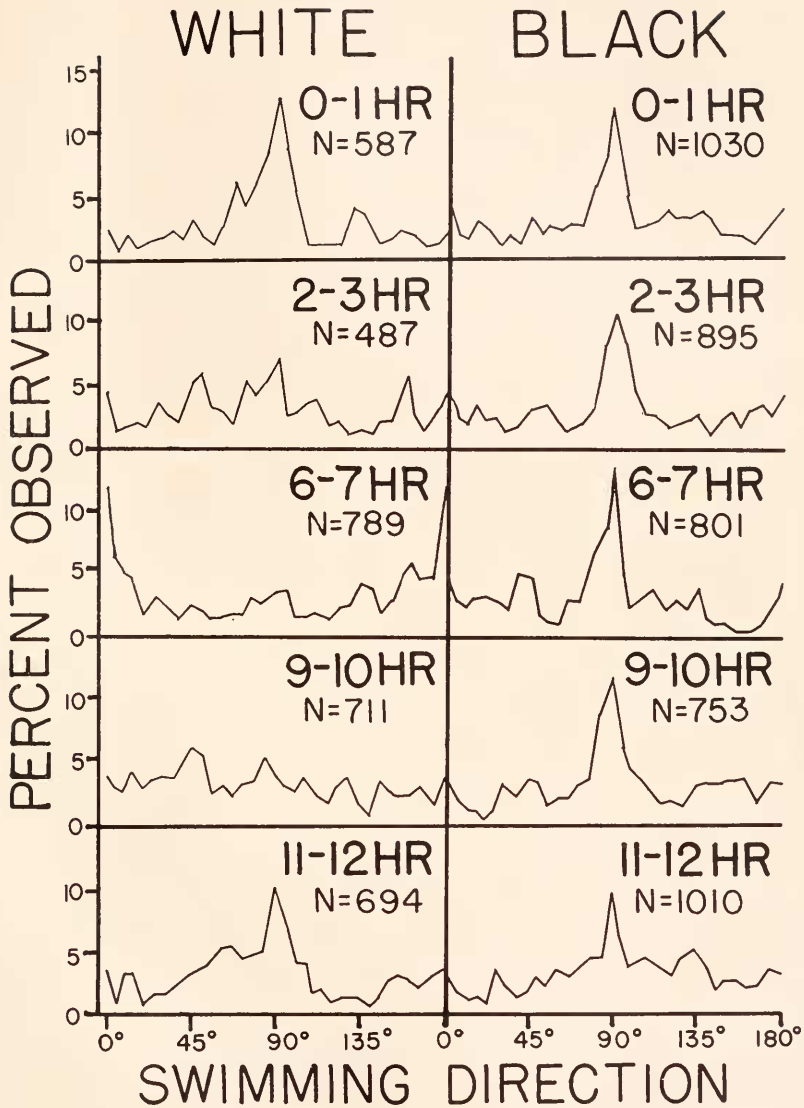The intensity of light was 1100 lux at the upper surface of the experimental cell.

FIGURE 1. Polarotaxis at different times during a 12-hour light cycle. Abscissa gives the angle between swimming path and plane of polarization. Ordinate gives the percentage of total swimming attempts. N gives the total number of swimming attempts. WHITE and BLACK denote the color of the sidewalls and diaphragm of experimental cell.

The vertical outer walls of the cell were covered with either black or white construction paper to minimize direct reflections from the walls. In addition, the walls were shaded from direct light with a circular black or white diaphragm having an aperture 20 mm. less than the inner diameter of the cell. The meniscus at the margin of the water surface was eliminated by pressing a flat glass plate against

the upper edge of the cell walls, thus sealing off the completely full vessel without an air-water interface. The water was filtered twice to reduce the differential scattering of polarized light by a turbid medium (Bainbridge and Waterman, 1958; Waterman, 1960).

Using this apparatus, the paths of the swimming copepods could be traced by following their projected images with a pencil on a piece of paper on the bench beneath the experimental cell. The plane of polarization was first set to one of four positions and noted on the paper along with the tracings. After a number of observations had been made, the plane of polarization was then changed at random to a new position and more tracings were made. A total of four different e-vector positions was used for each trial to eliminate the effect of any intensity or spatial cues in the cell.

The angle between the path of the copepod and the plane of polarization was then measured with a protractor at 1-cm. intervals along the length of each path tracing. The frequency distribution of the resulting angles indicates any relationship between the course of the copepods and the plane of polarization. Thus, if a copepod tended to swim perpendicular to the plane of polarization, a peak in the orientation readings would appear at 90° on the plot. The frequency distributions can be statistically evaluated as either random or with significant peaks by a chi-square test (Bainbridge and Waterman, 1957).

As indicated previously, *Cyclops vernalis* tended to cling to the bottom and sides of the experimental cell and only sporadically swam freely in the water.   In order to get a sufficient number of tracings in a 30-minute period, 20 copepods were placed in the cell to insure that one or two individuals would always be swimming. The paths of the copepods were recorded at 2-hour intervals throughout the 12-hour light period; no readings were attempted during the 12-hour dark period of the illumination cycle. In the following discussion, therefore, a time of 0–1 hours indicates the first hour after the light went on (experimental "dawn") and a time of 11–12 hours indicates the last hour before the light went off (experimental "dusk").   During each 1-hour period of observation, both black and white sidewalls and diaphragm were used to discover if any light contrast reactions were present as reported in several animals by Jander and Waterman (1960).

Results

When black sidewalls and diaphragm were used, *Cyclops vernalis* oriented at right angles to the plane of polarization at all times during the 12-hour light period. However, when white sidewalls and diaphragm were used, the same copepods in the same vessel at the same times of day now showed a regular 12-hour rhythm in polarized light orientation. Under these conditions, there was a 90° orientation to the plane of polarization at the beginning and end of the light period and a 0° orientation midway through the light period. These orientation peaks were statistically significant at the 0.5% level using a chi-square test. At intermediate times, however, orientation was poor and not significant statistically, appearing to be transitional between 90° and 0° orientation. The results for one such day are shown in Figure 1. The same results, using other groups of 20 copepods, were obtained on two other days when the experiment was repeated.

Polarotactic Behavior Under Simulated Natural Conditions

Introduction

In natural waters, the angle between the plane of polarization and the horizontal depends upon the line of sight of the observer, the position of the sun in the sky and the depth of the observer in the water (Waterman, 1954; Waterman and Westell, 1956). The plane of underwater polarization is always horizontal in horizontal lines of sight toward and away from the sun's bearing, but is tilted toward the sun in all other azimuths. The amount of tilting between the plane of polarization and the horizontal is maximal at right angles to the sun's bearing and is approximately equal to the sunlight's angle of refraction at the surface of the water. However, there is a decrease in the tilting of the polarization plane as depth increases.

At sunrise and sunset, when the sun is near the horizon, the angle of the plane of polarization may be as great as 45° along horizontal lines of sight perpendicular to the sun's bearing. At midday, when the sun is nearest the zenith, the plane of polarization along a line of sight perpendicular to the sun's bearing reaches its minimal tilt from the horizontal. In fact, when the sun is in the zenith, the e-vector is horizontal in all lines of sight. This then is the simplest pattern of natural underwater polarization and the most easily imitated in the laboratory.

Verheijen (1958) and Waterman (1961) have emphasized that much of the experimental work on light reactions of aquatic animals has been conducted under conditions atypical of those in open water. In the previously described experiment, the plane of polarization was directed vertically from above the experimental cell. This experiment might simulate polarotaxis in shallow waters where overhead sky patterns are directly visible over about 90°. However, such conditions of polarization are limited to shallow waters and could not model the effect of lateral illumination from underwater polarization in deeper waters.

Methods

In order to approximate more natural conditions in the study of polarotaxis, the following setup was employed: Fifty copepods were placed in a rectangular battery jar, 156 mm. deep by 100 mm. long by 80 mm. wide. Sheets of Polaroid were placed on each side of the jar so that the plane of polarization was horizontal along all lines of sight at all times of day. This simulates the simplest natural pattern described above. The jar was illuminated from above by unpolarized light. Both the vertical and horizontal illumination was provided by tungsten filament lamps, but their intensities were set in two different patterns.

In surface waters the light intensity from above is much greater than the light intensity from the sides. To approximate this in the laboratory, the light sources were adjusted such that the intensity from above was 1100 lux inside the battery jar and the intensity from the sides was 100 lux inside the battery jar. As depth increases in natural waters, the ratio of the vertical to horizontal illumination decreases (Jerlov, 1951). To approximate the pattern of light intensity found in deeper water, the light intensities from above and from the sides were made equal inside the battery jar and set at either 1100 lux or 100 lux.

The intensity of light was controlled with a rheostat and measured with a luxmeter. Since changing intensity with a rheostat can produce changes in the wave-length of the emitted light, any behavioral changes induced by different intensity patterns might be due to different reactions of the organism to different wave-lengths of light. To establish that this was not the case, the intensities were also varied by changing the distance of the light source from the battery jar; this procedure does not change the wave-length. It was found that similar results were obtained in this set of experiments and in all others requiring differential intensities regardless of the manner in which intensity was varied.

The swimming copepods were observed visually and their paths were tallied in the following way: On a clear piece of plastic a circle was drawn and divided into 16 equal parts by 8 lines drawn as diameters through the center. One of these diameters was chosen to represent an up-down axis; the diameter perpendicular to it represented a left-right axis. The other diameters represented intermediate directions. When a copepod began swimming freely in the water, the center of this circle was visually aligned to the copepod's starting point so that one of the axes of the circle closely approximated the path of the swimming animal. The paths were then recorded over a period of a half hour and a frequency diagram plotted. The angle between the path of the copepod and the plane of polarization could be estimated only roughly with this method. Any given excursion of a copepod from rest into the open water had to be approximately aligned to one of the reference axes on the plastic sheet; the error involved could be as great as 11°, but was generally much less. The copepods were observed at approximately 6-hour intervals throughout the course of the 12-hour light period.

Results

Using horizontal polarization to simulate natural conditions, the effect of the angular distribution of light intensity on polarotaxis was studied (Fig. 2). With a contrasting ratio of vertical to horizontal intensity (1100 lux from above, 100 lux from the side), polarotaxis was always primarily 90° to the horizontal plane of polarization with no rhythmic responses present. However, with a uniform angular distribution of light intensity (equal intensity from both the sides and above) of either 1100 lux or 100 lux, a rhythm was present at both intensities. Compared with a control group where no polarization was present, these copepods swam more vertically (at right angles to the plane of polarization) at the beginning and end of the 12-hour light period and more horizontally (in the plane of polarization) at the middle of the light period. This indicates that a uniform angular distribution of light intensity over a range of absolute intensities induces the diurnal rhythm in the polarotactic response.

Swimming in unpolarized light is basically horizontal at all times of day, but orientation is not precise. This is true in uniform intensity patterns of either 1100 lux or 100 lux and in contrast intensity patterns as well. The addition of horizontally polarized light both increases the precision of horizontal swimming and induces a periodic vertical swimming component. The control group further demonstrates that there are no rhythms in orientation in unpolarized light. Polar-
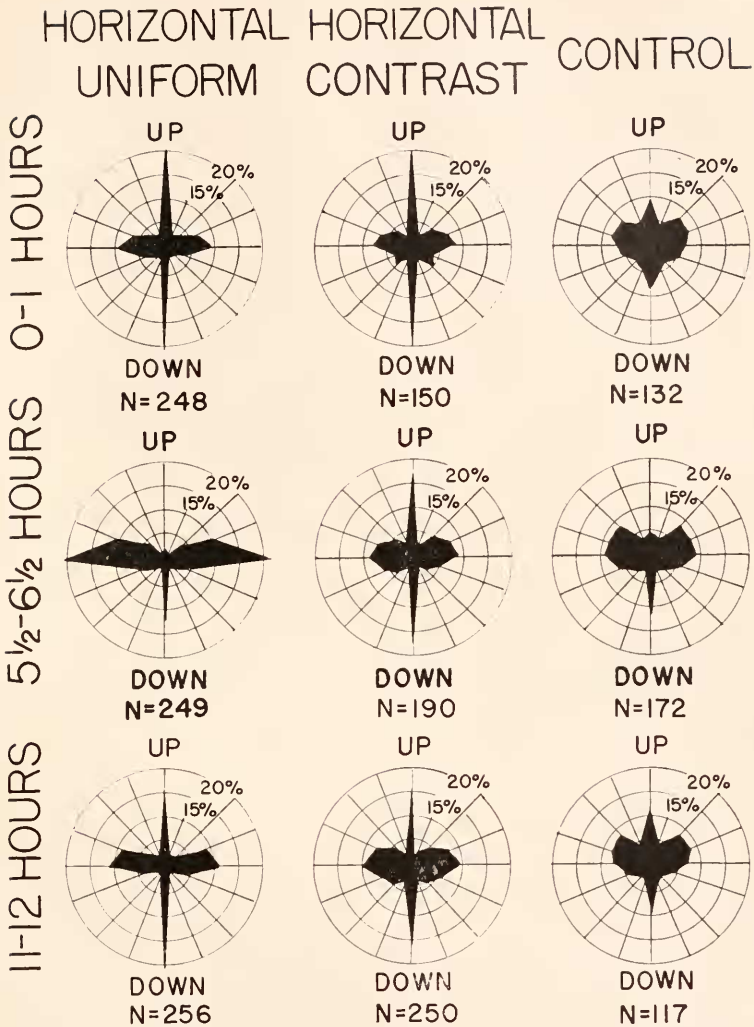
FIGURE 2. Orientation to horizontally polarized light at different times during a 12-hour light cycle. Radial axes represent direction of swimming with respect to gravity. Concentric circles represent the percentage of total swimming movements. N gives the total number of swimming movements. HORIZONTAL means horizontally polarized light was used; the plane of polarization is perpendicular to the UP-DOWN axis. UNIFORM means the light intensities from above and from the sides were equal. CONTRAST means the light intensity from above was greater than from the sides. CONTROL group had no polarization; angular distribution of intensity had no effect on this group.

ization must be present (along with a uniform angular distribution of intensity) to elicit a diurnal rhythm in the orientation behavior of these copepods. Furthermore, contrast and uniform angular distributions of light intensity elicit the same response (predominantly horizontal swimming) in unpolarized light, but each elicits a different response in polarized light.

In order to demonstrate conclusively that the observed rhythm in swimming behavior was not influenced by gravity responses, the lateral patterns of polarization were varied. The intensity in all cases was 1100 lux inside the battery jar from both above and from the sides. If the light from the sides was polarized in a vertical plane, instead of horizontally as above, the diurnal rhythm in polarotaxis still persisted, but now the copepods swam horizontally with respect to gravity (but still 90° to the plane of polarization) at the beginning and end of the light period and vertically with respect to gravity (but still 0° to the plane of polarization) midway through the light period.

If the plane of polarization was set at an angle of 45° to the horizontal on all sides of the jar, the coepods swam at an angle of 45° upwards and downwards with respect to gravity at all times of the day. The rhythm did not appear under these conditions since swimming at either 0° or at 90° to the plane of polarization both result in swimming 45° to the horizontal with respect to gravity. The frequency diagrams for these experiments are not figured in the paper since they can be adequately described verbally.

Polarotactic Behavior in Changing Intensities of Light

Introduction

All the experiments described so far indicate that polarized light merely orients swimming direction more precisely, either in a vertical, horizontal or 45° to the horizontal direction, but causes no net displacement of the population, *i.e.*, migration. Inspection of Figure 2 shows that given a population of *Cyclops vernalis* swimming primarily horizontally in unpolarized light, the addition of horizontally polarized light will alter the swimming behavior by inducing a vertically directed swimming component. However, this vertical component is equally divided into upward and downward fractions, causing no migration in the population.

Experiments on other planktonic organisms (Ewald, 1912; Clarke, 1930, 1932; Johnson, 1938; Johnson and Raymont, 1939) indicate that changing light intensities rather than constant illumination cause net displacements of the populations: increasing intensity causes a downward migration and decreasing intensity causes an upward migration when the light source is overhead. Similar changes have been observed in the deep scattering layer in nature (Hersey and Backus, 1962). This sound-scattering layer, composed of marine organisms, migrates upward at night and downward during the day, being greatly influenced by light intensity.

Methods

Since polarized light of constant intensity causes no migrations of the swimming *Cyclops vernalis*, the effects of intensity changes with and without horizontal polarization were investigated to see if net displacements could be elicited. Observations were made with either decreasing or increasing light intensities from above and/or from the sides to approximate the conditions at sunset and sunrise, respectively.

In cases of decreasing intensity, the initial intensity of light was 1100 lux and decreased by steps of 200 lux every ten minutes until a final intensity of 100 lux was reached. In cases of increasing intensity, the initial intensity was 100 lux and increased by steps of 200 lux every ten minutes until a final intensity of 1100 lux was reached. In addition, either the overhead and lateral lights changed intensity at the same rate (uniform angular distribution of intensity) or the lateral light remained constant at 100 lux while the overhead light changed in intensity (contrast angular distribution of intensity). The intensity of light was controlled manually with a rheostat and measured with a luxmeter as described previously.

Results

When polarization is not present, intensity changes caused no net displacements in the population; swimming remained primarily horizontal in all cases.
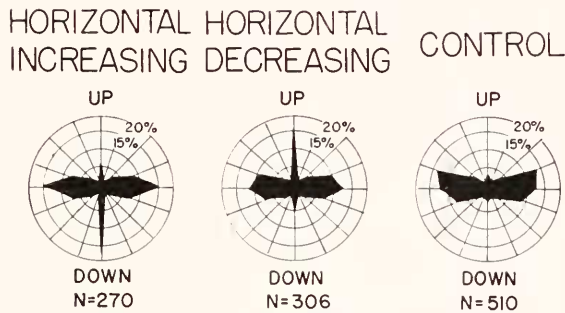

FIGURE 3. Orientation in changing light intensities. Method of diagramming is same as in Figure 2. HORIZONTAL means horizontally polarized light was used. INCREASING and DECREASING describe the change in light intensity. CONTROL group had no polarization; changing intensity of either type had no effect on this group. Time of day and pattern of intensity distribution had no effect on intensity responses.

Without polarization, then, orientation behavior in changing intensities was similar to that found with a constant intensity.

However, when the lateral light was polarized horizontally (Fig. 3), increasing intensity caused a net downward movement in vertically swimming individuals whereas decreasing intensity caused a net upward movement in vertically swimming individuals. Horizontally swimming individuals were not affected.

These results in horizontally polarized light held regardless of whether overhead and lateral lights changed intensity at the same or at different rates. The time of day also had no effect on the results; changing intensities always caused a vertical displacement of the population as long as polarized light was present. This indicates that the cue of changing intensity is stronger than the rhythm in polarotaxis that occurs when intensity is held constant: The $0°$ orientation to the plane of polarization that occurs at midday in a uniform intensity distribution of unchanging intensity is changed to a $90°$ orientation when changing intensities

are employed. However, since intensities are normally constant at midday in nature, the rhythm probably persists under natural conditions.

DISCUSSION

Ecological significance

From the experiments with *Cyclops vernalis* it is clear that experimental conditions including unpolarized light at constant intensity in all directions at all times of day are highly artificial. Extremely interesting patterns of behavior that would never occur under such highly artificial light regimes are elicited when certain aspects of natural conditions of illumination are simulated, even
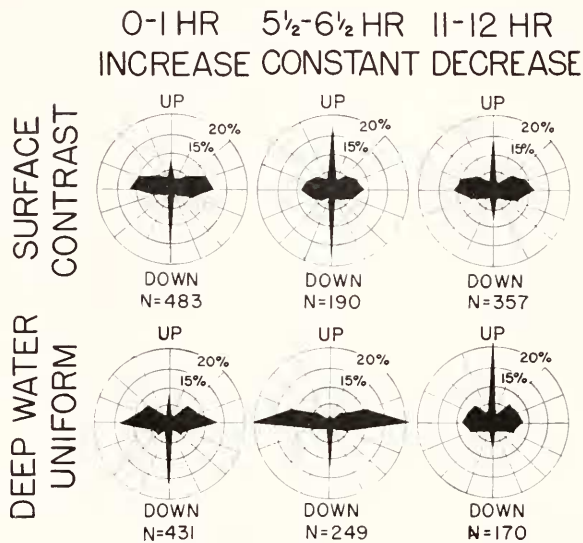

FIGURE 4. Summary of experiments using horizontally polarized light at different times of the 12-hour light cycle. Method of diagramming is same as in Figure 2. INCREASE, CONSTANT and DECREASE describe change in light intensity. CONTRAST describes intensity distribution found at the SURFACE of water. UNIFORM describes intensity distribution in DEEP WATER.

crudely. In order to understand the ecological significance of the various behavioral reactions of *Cyclops vernalis* to light, the various parameters of the experimental illumination must be given a natural interpretation.

In this study, a horizontal polarization of light along all lines of sight was used to approximate the simplest of natural patterns of polarization in the aquatic habitat. It must be emphasized that this is a pattern that occurs only in low latitudes around noon. Increasing intensities of light were used to simulate conditions occurring during the early morning hours whereas decreasing intensities were used to approximate the conditions of illumination at dusk; constant intensities were used to represent conditions at midday. The effects of depth on light

intensity patterns were crudely mimicked by changing the intensity ratio of the overhead and lateral lights and by the use of black or white sidewalls and diaphragm in the experiments using polarized light from above.

A summary of the experimental results is presented in Figure 4. Only those studies performed under conditions of illumination approximating those found in nature are used; those studies that elucidated the behavioral reactions but which have no natural counterpart (such as increasing intensities at the end of the light period) are omitted.

When all the experimental results are arranged in a natural sequence, the following trends appear: In the morning, swimming has a net downward component both at the surface and in deep water. A population behaving in this manner would tend to sink in the water. At midday, those copepods that sank into deep water in the morning would now move primarily horizontally in the water, maintaining their position in deep water. However, those copepods that remained at the surface during the morning would still tend to move vertically up and down at midday. Copepods moving vertically downward from the surface might eventually reach a more uniform angular distribution of light intensity, causing them to fan out horizontally.

In this way, the vertically swimming copepods found at the surface at midday would gradually be "trapped" by the deep-water angular distribution of light intensity, eventually causing this surface population to redistribute in deeper water. In the evening, swimming has a net upward component both at the surface and in deep water. This would cause the population to rise toward the surface in the evening. These trends in swimming behavior are consistent with the patterns of movement shown by many planktonic Crustacea in their vertical migrations. This implies that the parameters of illumination examined in this study may be very important for the orientation and release of migratory behavior in the aquatic habitat.

Physiological significance

If the foregoing interpretation of the experimental results with *Cyclops vernalis* is correct, then the physiological significance of the various parameters of illumination can be summarized as follows: The angular distribution of light intensity is a visual cue giving information as to the copepod's relative depth in the water. The plane of polarization is used as a frame of reference for orienting locomotor movements in the water where other orienting cues such as landmarks are sparse. By swimming at right angles to the plane of polarization, the copepod will move predominantly vertically at most times of day; by swimming in the plane of polarization, the copepod will move horizontally much of the time. Thus the polarization pattern of the aquatic habitat provides the copepod with vertical-horizontal reference coordinates with which to orient. Changing intensity of illumination provides migratory cues that lead to a net displacement of the population only when it is correctly oriented. Increasing intensity is a cue to swim downward, whereas decreasing intensity is a cue to move upward. The diurnal rhythm in polarotaxis that occurs only in deep-water uniform intensity distributions functions as a behavioral "trap" to keep the copepods in deep water during midday.

SUMMARY

1. A series of laboratory experiments on the fresh-water copepod, *Cyclops vernalis*, revealed an endogenous rhythm in its orientation to polarized light. The copepod swam perpendicular to the plane of polarization at the beginning and end of a 12-hour diurnal light period, but swam parallel to the plane of polarization midway through this light period.

2. The rhythm was not present under all experimental conditions, being released only when the intensity of light from above was equal to that from the side. Under other experimental conditions, the copepods swam perpendicular to the plane of polarization at all times during the light period.

3. A pattern of horizontal polarization, crudely simulating the simplest natural underwater pattern, was found to provide *Cyclops vernalis* with vertical-horizontal reference coordinates for spatial orientation.

4. Changing intensities of polarized light induced net displacements of the population, thus effecting vertical migration in the laboratory.

5. The ratio of overhead to lateral light intensity provided a visual cue indicating water depth. The diurnal rhythm in polarotaxis operated only with deep-water intensity ratios of horizontal and vertical light and served to orient deep-water individuals in a horizontal plane at midday, thus inhibiting vertical swimming patterns (which occur at dawn and dusk) that might carry them to the surface at that time.

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